

nature, the incredible labours of scientists would be without hope. We must just soldier on in that faith to whatever end it may ultimately lead.

Reference -

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THE BIOLOGY OF THE LILAC LEAF MINER,

GRACILLARIA SYRINGELLA FABR. (LEPIDOPTERA:GRACILLARIIDAE)

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The life history of Gracillaria syringella Fabr. was followed from 1963 to 1965. The habits of the various stages were noted, especially the way in which the larvae mined and rolled the lilac leaves. Population estimates were made in a small area in Calgary. Two ichneumonid parasites were found, Scambus hispae (Harris) and Itoplectis quadricingulata (Provancher). The effects of the lilac leaf miner on its host plant were noted. The world distribution of G. syringella and its dispersal in North America are discussed.

Gracillaria syringella Fabr., the lilac leafminer, is of European origin and is widely distributed in Europe. It was first recorded from North America in 1923. The lilac leafminer has become an abundant and widely distributed major pest of lilac (*Syringa* sp.) through middle North America in the past 40 years. It is not restricted to lilac although this is the most common host in America; privet is also attacked. In Europe *G. syringella* is found on ash as well as lilac and privet.

In the 19th Century the lilac leaf miner received a great deal of attention. Many superficial reports of the habits of this insect were published. Since 1900 very little has been added to the literature on *G. syringella*.

Adults reared from larvae collected in Calgary were sent to the British Museum of Natural History and were identified by J. Bradley as *Gracillaria syringella* Fabr.

I have attempted a complete biological study of *G. syringella*, including its life history and habits, parasites and predators, dispersal in Alberta, distribution and spread in North America.

GEOGRAPHICAL DISTRIBUTION

History and Distribution of Lilac

Lilacs, in the genus *Syringa* of the olive family, Oleaceae, are an Old World group of shrubs and small trees confined mainly to Asia and having no indigenous representatives in the New World. There are 28 species of lilac recognized by McKelvey (1928), the most popular ones being the common lilac, *Syringa vulgaris* Linnaeus (1753) and the Persian lilac, *Syringa persica* Linnaeus.

From evidence collected by McKelvey (1928) on the geographical distribution and history of the common lilac it appears to have originated in the mountains of the Balkan Peninsula. A plant, identified by Lecluse in 1576 as *Syringa vulgaris*, was first mentioned in the literature by Pierre Belon, the French naturalist, in 1554 while he was in Persia. It is not known when the common lilac was first brought into cultivation in Europe but it was taken, probably to Vienna, from Constantinople not later than 1563. It was cultivated in Paris in 1601 according to Franchet (1891). From gardens it escaped into the hedge rows and grew wild. It soon came to be regarded by botanists as indigenous to various countries of western Europe. By 1629 it was cultivated in both the white and purple-colored forms in England.

The Persian lilac is said by McKelvey (1928) to have originated on the mountains of southern Kansu, in central China. From here it was carried to Persia where it became naturalized on hill slopes and by 1620 it was also known to be in cultivation in Venice. The Persian lilac is the greatest wanderer of all the species of lilac and it is, with the common lilac, parent of the first hybrid lilac, *Syringa chinensis* Willd., better known as *S. rothomagensis* Poiteau and Turpin, 1808, which appeared in the Botanical Garden at Rouen, France about 1777. Various species of lilac are now found all over the temperate regions of Europe and Asia, including such islands as Japan and Great Britain.

The date of introduction of the common lilac to North America is uncertain. While the probability is that it came over with the early settlers, there is no authentic record of it growing here before the last half of the 18th Century. Today it has spread over most of the populated area of the temperate zone of North America.

Distribution of Ash and Privet

The other host plants of the lilac leaf miner are less commonly infested. The genera *Fraxinus* (ash) and *Ligustrum* (privet) also belong to the olive family, Oleaceae. Their distribution in the Eastern Hemisphere is very similar to that of lilac though they extend slightly further south into Malaysia. Ash is common throughout Canada and the United States; both ash and privet extend further south than lilac. Privet extends less far north; in Canada it is only abundant on Vancouver Island and along the Great Lakes and St. Lawrence River.

Lilac leaf miner infestations on Vancouver Island were observed during the autumn of 1964 and were as abundant on privet as they were on lilac. Infestation of ash was neither observed nor reported to me during the three years of this study. The most common species of ash

infested in Europe, *Fraxinus excelsior* has never been introduced in any quantity into North America, being used only occasionally as an ornamental.

History and Distribution of *Gracillaria syringella* Fabr.

The geographical distribution of its host plants, lilac, privet, and ash, though it does not occur throughout the host range.

Gracillaria syringella Fabr. was noticed by Reaumur in France in 1736. Lilac had been there for at least 140 years so the leaf miner was possibly present long before Reaumur saw it. Stainton remarked in 1864 that the species were plentiful in England, France, Germany, and Switzerland. Today most other countries of Europe and Asia can be added to this list. Those countries from which no records are available, such as China, Norway, Belgium, Spain, Portugal, Hungary, and the Balkan countries may also have the insect.

As the first accounts of the lilac leaf miner in North America were from four localities; Toronto, Newcastle, Guelph, and Ottawa, the insect must have been present at least a year before this (1923), probably several, to have covered such a large portion of southern Ontario. It was reported in 1924 from the Puget Sound area of the State of Washington. From these first incidences the area covered by the leaf miner rapidly expanded. On the west coast by 1927 it had spread to Vancouver Island where it was reported from Victoria and Sydney. It reached the city of Vancouver in 1928 and the Okanagan Valley by 1941. By 1960 it was established in Calgary, Alberta. In the east its range included Quebec by 1925, New Brunswick by 1938, Nova Scotia by 1939 and Newfoundland by 1943. It also occurs on Prince Edward Island. In the western United States it was reported from Moscow, Idaho in 1939 and in the eastern United States *G. syringella* had reached Mt. Desert Island in Maine by 1932. It was found in Philadelphia and New York in 1928 and was well established in northern Vermont by 1936.

Today the leaf miner's distribution in North America has expanded to include most of the southern half of Canada except for Saskatchewan and Manitoba where there has been only one report, from Winnipeg, 1965. Included also is the northern half of the United States except for a strip extending south from Saskatchewan and Manitoba through North Dakota, South Dakota, Nebraska and Kansas (figs. 1 and 2).

G. syringella is well established in southern Alberta and has been found as far north as Edmonton. It was found in small numbers in Edmonton during 1963 and during 1965 was present here in infestation proportions. It may be expected to continue spreading northward and eventually reach the northern limit of the host plant, lilac, as it has done in Russia (Strokov 1956).

The lilac leaf miner appears to have been introduced to both coasts of North America at approximately the same time. It probably entered in the pupal stage in soil around the roots of imported lilac shipments. Prior to the prohibition of the movement of soil on plants from Europe to Canada in May 1965, evergreen trees were shipped in soil or peat moss and deciduous trees were usually shipped barerooted, though lilacs, particularly the French hybrids, were often imported in soil balls. Imported



Fig. 1. Known distribution of the lilac leaf miner in Canada to end of 1964.

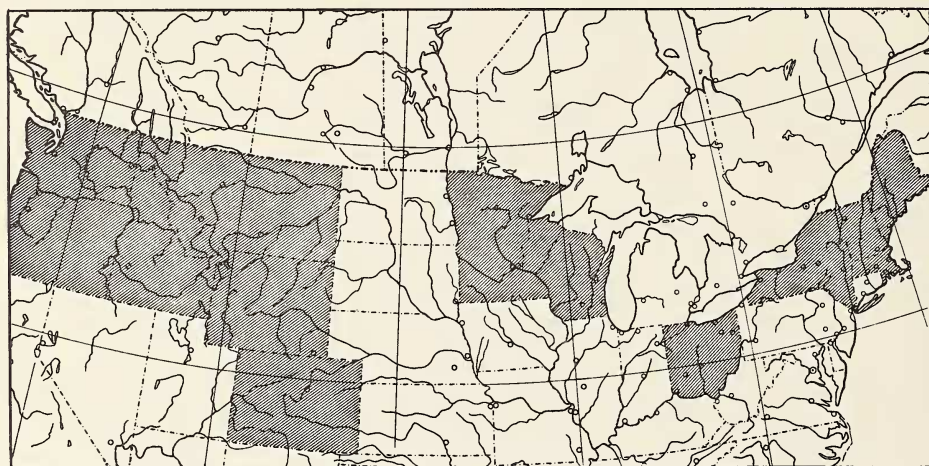


Fig. 2. Distribution of the lilac leaf miner in the United States to end of 1964.

lilac today is packed in peatmoss after the leaves have dropped. The soil around the roots is removed so it is unlikely that leaf miner pupae are still transported with nursery stock.

Differential Attack of Host Plant Species by the Lilac Leaf Miner

Not all species of lilac, ash, and privet are infested in Europe and those species which are infested are not attacked equally. The species were separated into four categories according to their susceptibility to *G. syringella* attack:

Heavily Infested

Syringa vulgaris L.
Syringa pekinensis Ruprecht
Syringa josikaea Jacq.
Fraxinus excelsior L.
Fraxinus excelsior L. var. *monophylla*

Lightly Infested

Syringa persica L.
Syringa villosa Komarov
Syringa emodi Wallich
Syringa reflexa Schneider
Fraxinus rotundifolia Mill. var.

Ligustrum japonicum Thunb.

Ligustrum ovalifolium Hasskarl

Ligustrum californicum Hort. ex Decne
(= *ovalifolium* Hassk.)

Fraxinus potamophila Herd.

Ligustrum vulgare L.

Slightly Infested

Fraxinus americana L.

Fraxinus pubescens Lam. ex Bosc

Fraxinus pennsylvanica Marsh.

Less Heavily Infested

Fraxinus excelsior L. var *diversifolia*

The situation in North America is similar except that none of the *Fraxinus* (ash) species in North America are attacked and *Ligustrum vulgare* should be placed in the heavily infested category.

C. B. Hutchings (1925), in Canada, made a similar list for varieties of *S. vulgaris* from the Arboretum at the Central Experimental Farm, Ottawa where over 150 varieties were grown. He observed that the lilac leafminer showed a marked preference for some varieties while avoiding others entirely.

MATERIALS AND METHODS

Preliminary studies were carried out in both Calgary and Edmonton during the summer of 1963 and the timing of the life cycle in Alberta was determined. *Gracillaria syringella* infestations proved to be much more extensive in Calgary than in Edmonton so further studies were done there.

The main study area consisted of the lilac bushes located in northeast Calgary (fig. 3). It was necessary to be close to the outdoor experiments at all hours. Ten lilac bushes of approximately equal size (seven feet high and three feet in diameter) were used for most observations. Three of the bushes, group A, were situated against a fence and were partially shielded from winds by houses and trees on either side. One of the bushes, B, was shielded from all except south winds. It was exposed to the sun most of the day and had warmth from the house on two sides; the larvae developed more quickly here than on the other bushes. Groups C and D were shaded much of the time by houses on both sides.

In 1964 collections of ten leaves from each of the 10 bushes were made every six days during the spring generation and every three days during the second generation. The leaf collections were not random, but both mined and unmined leaves were included in the sample which was taken as follows. Areas were chosen from different sides of the bush; the inner and outer layers, upper and lower sections. The leaves picked from these areas with eyes closed, were preserved in alcohol and examined the following winter. As it took at least 20 min to search each mine this could not be done immediately. In preliminary examinations it was noted whether the leaves were mined or rolled; if they were mined, the size of the mines was estimated. The larvae inside were counted and their head capsules collected from the molt skins and measured to estimate the age of the larvae. The dead larvae were counted. Both the

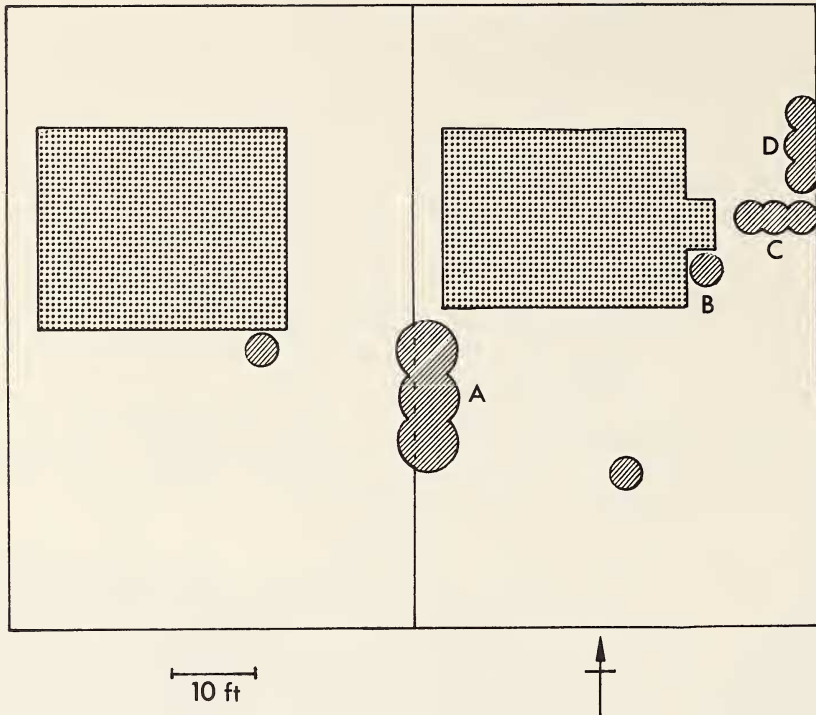


Fig. 3. Study area showing positions and orientation of lilac bushes.

live and dead larvae were examined for external and internal parasites. Internal parasites could be seen through the cuticle and were dissected out. All parasites were mounted on microscope slides. The interior of the mine was examined for signs of mould, predators, and bird pecks. The patterns of larval frass were also observed.

Temperatures were recorded with a thermograph under the middle bush of group A during the summer of 1964. Since these temperatures differed little from those recorded at the Calgary Municipal Airport, the airport records were used for 1965. Other lilac bushes in the immediate vicinity were sampled for estimating moth populations and for dispersal experiments.

Field observations began 14 May, 1964 when several moths emerged on a lilac bush away from the main study area, but collections did not begin until 26 May when moths began appearing in the bushes under observation. Collecting continued until 1 October, 1964 and observations continued until all the leaves had dropped off on 23 October. Attempts to rear moths on lilac suckers in caged pots were unsuccessful.

Although the moths were most active during the early morning and in the evening they were easiest to catch then because they appeared to be less sensitive to slight movements of the leaves and shadows as vials were placed over them. Ten-dram plastic vials with snap-caps were used to catch the moths singly or in pairs; in these they could be quickly sexed without handling. The external genitalia were examined under a binocular microscope (X 12). This was easier than using the frenula of the wings.

Larvae and eggs were collected by picking leaves off the lilac bushes and opening the mines in them. Larvae were also caught as they spun their silken threads and descended to the ground on them. During pupation aluminum pie pans (8 inch diameter of soil-covered area) filled with soil were kept under the bushes of group A (fig. 4) and the descending larvae burrowed into the soil and pupated. After dropping had ceased, the pans were put individually into muslin bags to await emergence of the adults. The emerging moths were counted and the pans searched for those larvae and pupae that failed to complete development.

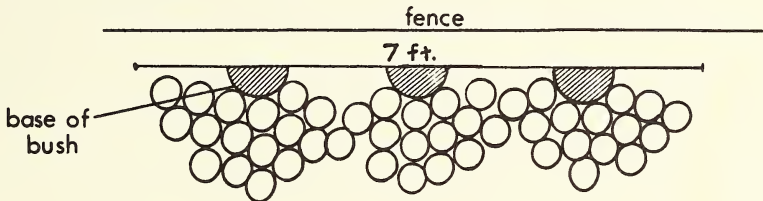


Fig. 4. Positions of aluminum pans under group A bushes.

In estimations of moth populations and dispersal experiments there was some difficulty in finding a substance with which to mark the moths that could be readily seen and yet would not hamper their movements. Many colored powders, both dry and in solution, were tried but the most suitable was Fluorescein (free acid), (Allied Chemical Corporation, National Aniline Division) which sticks to the body and wing scales. The powder was applied by placing a small amount in a jar with twenty to thirty moths and then gently shaking it. Care was taken not to get too much powder on the moths as they were killed if the layer of powder on them was too thick. In the laboratory, caged moths with fluorescein on them lived a normal length of time with no observable ill effects. The dye particles were red and showed up easily with only a cursory inspection of the captured moths.

In the laboratory two methods were used to rear the larvae. One method consisted of placing the lower end of a twig or small branch with six to ten leaves on it into a small container of water. The top of the water container was then sealed with tape to prevent descending larvae from drowning and to slow evaporation. The container and twig were then put into a larger glass cage covered with muslin. In the other method one leaf was placed on a very moist piece of cotton in such a way that any cut edge, such as the petiole tip, was embedded in the cotton. This was then put on a filter paper which was moistened every other day, in a covered, plastic petri dish. Excessive moisture was avoided

as it encouraged mould formation. Pupae were kept both in the petri dishes and in glass jars partially filled with soil. The jar openings were covered with muslin rather than lids to prevent condensation.

Microscope slides were made of all parasite eggs and larvae using methyl blue dissolved in polyvinyl lactophenol (Esbe Laboratory Supplies) as a stain and mounting agent.

MORPHOLOGY AND LIFE CYCLE OF *GRACILLARIA SYRINGELLA* FABR.

Description of Stages

Egg

The transparent chorion of the flattened, prolate spheroid egg has a reticulate surface with roughly pentagonal areas separated by ridges. As the egg develops it becomes opaque and the curled embryo can be clearly seen within. Dimensions (Table 1) were similar to those previously obtained by Pussard (1938) - 0.5 mm x 0.2 mm, in France and Maar (1932) - 0.42 - 0.54 mm x 0.19 - 0.26 mm, in Estonia.

Larva

There are five larval instars, the first three mine the leaves and the last two roll them. Table 1 contains measurements of the larval instars.

First instar - A newly hatched larva consists of a head and 13 other segments; 3 thoracic segments and 10 abdominal segments, the 10th very small. The flattened, wedge-shaped, prognathous head capsule is relatively large. The cuticle is transparent except for the heavily sclerotized mandibles which are light brown. The body contents are also almost transparent, all that can be seen without special lighting is the gut. There are no legs or prolegs but the thoracic segments bulge laterally more than the abdominal segments, aiding locomotion in the mine.

Second instar - The head of the second instar larva is still wedge-shaped and prognathous. The translucent body is flattened and similar to that of the first instar.

Third instar - In contrast to the first and second instars, the head of the third instar larva is spherical and hypognathous. Hypognathous heads are recorded by Tragardh (1913) as typical of external feeding larvae but the third instar *G. syringella* larva still feeds in the mine. Silk is secreted from a median spinneret on the labium and is used to pucker the mine walls, producing greater depth for the now cylindrical larva. The body appears light green because of chlorophyll in the gut. There are three pairs of thoracic legs, each leg composed of three short segments and terminating in a long claw. There is a pair of prolegs on abdominal segment 3, 4, 5 and 10. The prolegs have one or two rings of crochets on them; the arrangement of these is described under adaptations of larval morphology for mining.

Fourth instar - The body is cylindrical and still appears green from color in the gut. The head capsule is light brown, through darker than in the third instar. The mouthparts are of the external feeding type but larger and better developed than those of the third instar. The spinneret

is larger in proportion to the size of the head capsule than in the third instar probably because a stronger silk is required to roll the leaf around the larva which has now emerged from the mine.

Fifth instar - The body color of the fifth instar larva changes from green to a yellowish-white as it matures and stops feeding. The body is cylindrical with numerous bristles. Fulmek (1910) constructed a setal map and provided a complete description as shown in fig. 5. The head is hypognathous and a medium brown color.

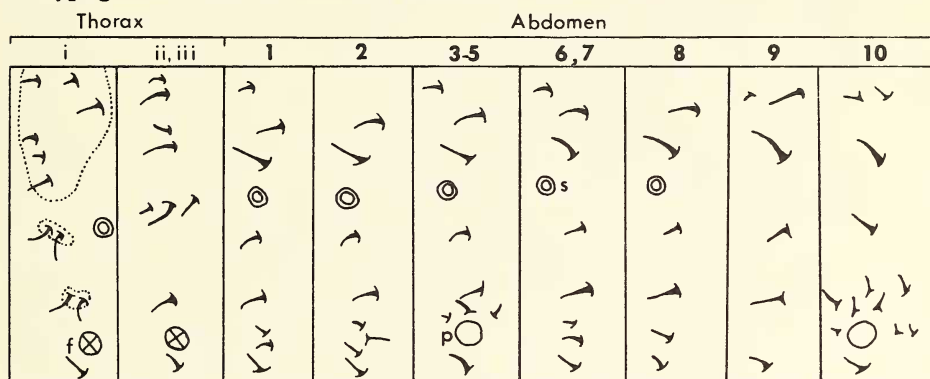


Fig. 5. Setal patternmap of fifth instar larva of *G. syringella*- lateral view
x 20 f = thoracic foot, p = abdominal proleg, s = spiracle(after Fulmek).

Pupa

In the laboratory, without soil, the pupa is found inside a white silk, oval cocoon measuring 7 to 10 mm in length. The cocoon, as it is spun naturally under the surface of the soil, becomes covered with soil particles and debris. The pupa is light brown. Its mouthparts, antennae, wings and legs lie flat against the body but are not fused to it, though they are fused to each other. Two pairs of legs are totally fused to the wings while the metathoracic pair extends beyond the wing tips. The galeae extend beyond the first two pairs of folded legs, almost to the wing tips. The antennae lie lengthwise, reaching to the end of the last abdominal segment. The pupa is capable of considerable movement and if disturbed a vigorous reaction may be set up in which its abdomen is bent rapidly from side to side. The pupa has a sharp point at the anterior end which pierces the cocoon as it wriggles all except the last few abdominal segments free of the cocoon before emergence of the adult (fig. 6).

Adult

The adult has the characteristics of the genus *Gracillaria* as described by Forbes (1923). The species *syringella* is not included in his key. The adult of *Gracillaria syringella* can be readily identified by the color of its anterior wings. They are a variegated mixture of grey, gold, and brown with six oblique bands of yellowish-white. The three apical bands are outlined in black. The wing span varies from 11 mm to 12 mm. The forewings are narrow, the width at the broadest point is 1 mm, almost doubled in the distal half by a fringe of long fine hairs. The posterior wings are shorter, 10 mm spread, and narrower, 0.75 mm. They are

almost surrounded by a fringe of long, light grey, very fine hairs. The underside of both pairs of wings is light grey.

The head is covered with long, smooth, somewhat erect, white and grey-brown scales, producing a variegated appearance. The maxillary and labial palpi are also a variegated grey; they are large and project upwards in front of the head (fig. 7). The galeae form a proboscis 4 mm long which is held curled at rest. The filiform antennae extend to the wing tips when the moth is at rest.

The body is completely covered with grey scales, those on the ventral side being almost white. The abdomen is 3.5 to 4.0 mm in length and 1 mm wide.

The legs are also completely covered with scales, those on the middle tibiae are more dense giving them a bushy appearance. On the posterior tibiae there are two pairs of spurs, one pair is one-third of the distance from the proximal end and the other pair is distal in position. The middle tibiae have only the apical pair, the anterior tibiae none. Each pair of spurs is asymmetrical, that spur nearer the body being longer. The femora are greyish-brown, the anterior pair rather darker than the other two pairs. The anterior and middle tibiae are dark brown, the posterior tibiae are paler. The anterior and middle tarsi are whitish with a few brown patches and the posterior tarsi are whitish-grey, more or less checkered with pale brown patches.

The moths at rest have the thorax elevated by the long legs. The anterior pairs of legs are held widely separated and directed forward. The posterior legs are placed against the sides of the abdomen with the longer inside spurs curving under it.

The genitalia have not been described.

TABLE 1. Sizes of various stages of *Gracillaria syringella* in mm.

Stage	Length	Width
Egg	$0.46 \pm 0.04^*$	0.22 ± 0.02
	(76)	(17)
	0.36 - 0.52	0.18 - 0.24
1st Instar	0.94 ± 0.32	0.18 ± 0.01
	(38)	(40)
	0.44 - 1.36	0.16 - 0.20
2nd Instar	1.62 ± 0.40	0.26 ± 0.02
	(40)	(40)
	0.88 - 2.20	0.20 - 0.28
3rd Instar	2.44 ± 0.45	0.35 ± 0.02
	(32)	(40)
	2.08 - 3.60	0.32 - 0.38

4th Instar	4.58 ± 0.61 (31) 3.12 - 5.72	0.54 ± 0.03 (40) 0.48 - 0.60
5th Instar	5.76 ± 0.73 (27) 4.40 - 8.00	0.76 ± 0.03 (34) 0.68 - 0.80
Pupa	4.87 ± 0.31 (6) 4.40 - 5.36	
Adult ♂ - excluding antennae	4.67 ± 0.33 (10) 4.17 - 5.17	
- apparent length with wings folded	5.92 ± 0.26 (10) 5.50 - 6.42	
Adult ♀ - excluding antennae	4.83 ± 0.22 (9) 4.41 - 5.08	
- apparent length with wings folded	6.00 ± 0.24 (9) 5.75 - 6.50	* Mean ± S.D. (No. of readings) Range



Fig. 6. Ventral view of pupa of *G. syringella*.



Fig. 7. Lateral view of head of ♀ *G. syringella*, x 50.

Life Cycle and Habits

Habits of the Moth

In Calgary lilac leaf miners overwinter as pupae in cocoons at the surface of the soil under debris and up to 1.5 cm below the surface. The depth of the pupae, according to Stokov (1956), varies with the hardness of the soil. In Russia he found pupae up to 5 cm deep in soft soil, 1 cm to 3 cm deep in heavy soil and at the surface in very hard soil. Emergence of adults in the spring from overwintering pupae was first observed in Calgary on the 19 May in 1963, 26 May in 1964, and 27 May in 1965. Emergence continued in all three years for about 20 days and moths were seen for an average of 33 days. This contrasts with the situation in Russia from 1937 to 1939 around Moscow and Leningrad. The earliest moths appeared on May 20 and they were last seen flying on June 9 (Stokov 1956). In France the moths that emerged in the spring of 1928 were observed to fly for 25 days (Pussard 1928). Stokov (1956) found that females lived from 5 to 7 days. In the laboratory I found newly hatched females lived from 8 to 14 days or an average of 10 ± 2.3 (18) days while males lived from 3 to 5 days or an average of 3.5 ± 0.8 (13) days.

Feeding by *G. syringella* adults has never been reported. In the laboratory flowers and sucrose-water solution on cotton were offered but the moths were never seen to feed although watched for prolonged periods. Other moths (50) given only water on cotton lived just as long. On five occasions an adult was seen to extend the proboscis and three had a drop of sticky substance on the tip. The guts of five wild-caught moths were ground up in Benedict's solution and heated. The mixture turned orange indicating the presence of reducing sugar. The experiment was repeated with the guts of five laboratory-raised moths that had access to sucrose solution. A positive result was again obtained, suggesting that some of the moths had fed.

Mating

The newly emerged adults mate at once. Mating takes place on grass blades, tree trunks and branches and on the lower surface of lilac leaves, also on objects such as a nearby fence and leaves of other trees. The moths, following emergence from the soil, were observed to make their way up to the tips of grass blades where they remained, waving their antennae. If a moth of the opposite sex walked up the same grass blade, it turned around before reaching the first one so that their anal ends made contact and mating occurred. Mating took place in the shade of the bushes or during evening hours rather than in direct sun light. In nature I observed copulation to last from a few moments up to at least 25 minutes. Mating was difficult to observe for long in nature because the pairs walked away from the original grass blades, while still in copulation, and were lost to view. In the laboratory copulation was observed to last from 25 minutes up to three hours. Pussard (1928) thought it lasted a minimum of four to five hours while Theobald (1905) reported at least two matings of 12 to 14 hours.

Oviposition and Fecundity

Strokov (1956) found that newly emerged, laboratory mated females, under laboratory conditions, could lay up to 248 eggs each. Six field-caught females from June 18, 1965 contained from 44 to 160 eggs each, an average of 94 eggs per female. They may have already oviposited. Muslin bags were placed around branches of growing lilac bushes. The leaves so enclosed were free of eggs. Four newly emerged and laboratory mated females were placed individually in bags. They laid from 135 to 170 eggs each, an average of 155 eggs per female. Twelve female moths field-caught on the first day of emergence in 1964, caged with one male each, in the laboratory, laid from 53 to 191 eggs each. The mean number of eggs per female was 111. These moths were seen to mate, almost immediately, once each but they could have mated again as the males lived for several days.

A female ready to lay eggs walks about on the lower surface of the leaf, her abdomen in contact with the epidermis. When she has found a suitable oviposition site she lays her eggs in rows alongside of a vein. Each egg slightly overlaps the one laid before it and each is glued to those on either side. The eggs, being transparent, are not noticeable in their normal position on the leaf in the shade but they can be seen with the naked eye in direct sunlight because the chorion reflects the light. They are usually placed close to a vein, only 5% of the masses found were near the leaf margins. 56% of the masses were placed close to the midvein and the other 40% were placed near the main lateral veins. Määr (1932) working in Estonia obtained similar results: 50% next to the midvein, 49% by main lateral veins and 1% beside secondary lateral veins. The mean number of eggs per mass is 7 ± 2.9 (100) with a range from 3 to 19. Strokov's (1956) results from Russia were comparable: 2 to 20 eggs, average between 5 and 6. Pussard (1928) thought that tactile setae on the tip of the female moth's abdomen detect the ridge of the vein and this releases the egg laying reflex, the ridge acting as a guide to the oviposition site. Pussard suggested that oviposition was only initiated by contact with a vein of a certain size, if it was too high, as in an old leaf, the site was bypassed, if it was too low the site was also bypassed. This mechanism would account for the fact that very young leaves or sites too near the leaf margin are avoided. When eggs were laid in the laboratory on the smooth, glass walls of the cages the rows were irregular or the eggs were in clumps and not as they are along a vein in regularly placed rows.

Egg Development

The duration of the egg stage under laboratory conditions at a temperature of about 70 F is from 4 to 8 days or an average of $5\frac{1}{2}$ days. Under natural conditions in the spring at a temperature of about 56 F the egg stage lasts from 7 to 17 days, or an average of $7\frac{1}{2}$ days. Pussard (1928), under laboratory temperatures of 59 F, found that the eggs took nine days to hatch.

The percentage of egg hatching is high. From samples of 2,000 eggs observed in the field it was found that during the spring generation, under natural conditions, 84% of the eggs hatched. Under laboratory

conditions the percentage of hatching was 91%, from a total of 420 eggs collected during the same generation. The 9% which did not hatch in the laboratory may not have been fertilized. There was never a whole mass of eggs remaining unhatched; only scattered eggs appeared inviable. Unhatched eggs remained transparent and flattened out. Empty egg shells were also transparent and flattened out but had frass trails leading from them. The difference between the laboratory and field results may have been due to predation by unidentified mites which were seen in the field. In laboratory tests, however, the mites could not be induced to feed on *G. syringella* eggs. No egg parasites were ever found and none of the unhatched eggs appeared damaged by larger predators. There was no mold observed on the eggs. The reduced hatch in the field is unexplained.

Larval Development

The egg is oriented with the larval head away from the leaf vein. The ventral tip of the egg is cut open by the mandibles and the larva chews through the chorion, which touches the epidermis, straight into the lower leaf epidermis without being exposed on the leaf surface. If the larvae hatch from eggs laid on the upper surface of the leaf (0.1% of the eggs), they are able to survive. Oviposition on the lower surface probably evolved because eggs laid here are sheltered and because there is no thick cuticle. The epidermal mine of each newly hatched larva proceeds in a straight line for a short distance. As the eggs of a mass hatch at approximately the same time and all the larvae proceed straight forward, usually all the mines join, producing one common mine for each egg mass. The first instar larvae in this mine feed gregariously in compact clusters around the edge (see fig. 8), producing a blotch after they have moved obliquely upwards into the palisade parenchyma. The second instar larvae feed alone though still in the common mine, in the palisade. The cylindrical third instar larvae consume the palisade, and parts of the spongy parenchyma, enlarging the mine. The fourth instar larvae leave only the upper and lower epidermis, then eat a hole through the thin mine wall and come out onto the lower leaf surface. They roll the leaf as described below. The fifth instar larvae live in the rolled leaf before descending to the ground on silken threads.

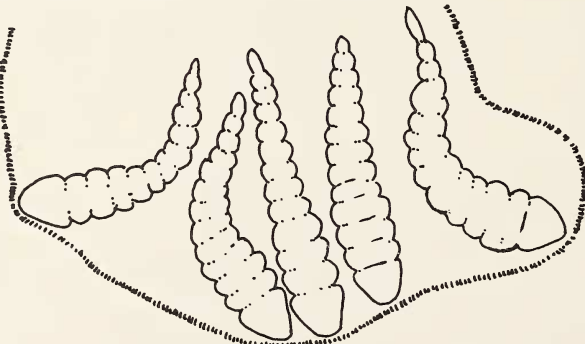


Fig. 8. Gregarious first instar larvae in mine,
x 80.

The larvae on the ground wriggle around until they have reached satisfactory pupation sites where they construct cocoons. In the laboratory it took about 24 hours for them to build a cocoon and another 12 hours for pupation to be completed. When emergence time approaches, a pupa wriggles, pushing on the end of the cocoon until it is pierced by the tooth on the head of the pupa. The pupa is almost free of the cocoon before the moth emerges. Emergence of the moths developing from the eggs laid in the spring was first observed in Calgary on the following dates: 28 July 1963, 27 July 1964 and 3 August 1965. Moths were seen flying during 1963, 1964, and 1965 for 54 days, 50 days, and 53 days respectively.

A second or summer generation of *G. syringella* begins with eggs laid by the spring (first) generation female moths. During the years 1963-1965 the earliest eggs were observed on 28 July, 27 July, and 3 August respectively. The larvae developing from these eggs pupated on 1 September, 14 September and 5 September respectively. The average duration of the egg and larval stages in the second generation over the two years of 1964 and 1965 was 42 days. In the same two years the duration of the egg and larval stages for the first generation was 41 days. The pupae remain as such until the following spring (about 37 weeks). Table 2 gives the duration of the separate larval instars for the spring (first) generation. The spring generation of most mining insects develops more rapidly than the autumn generation. According to Hering (1951) this is because the temperature is higher and the leaf cells have a higher protein content and are softer at the beginning of the growth period. Table 3 shows this does not always apply to *Gracillaria syringella* in Calgary. Although the cumulative temperatures in Alberta are higher during the first (spring) generation than during the second (autumn), the eggs are not laid on tiny, new leaves. The leaves must reach a minimal length of 35 mm before the moths will oviposit on them. Out of 500 measured leaves ranging in length from 30 mm to 104 mm, no leaves shorter than 35 mm had eggs on them. So the difference in the quality of the food between the two generations may not be great. This is also shown by the fact that the frass pellet size and amount voided are approximately the same in both generations and not, as Hering (1951) reported, greater in the second generation. The threshold temperature in Table 4 was taken as 40 F to calculate degree days of development.

HOST PLANT SELECTION

Gracillaria syringella is an oligophagous insect. In addition to the three susceptible genera of the family Oleaceae: *Syringa*, *Fraxinus* and *Ligustrum*, the larva is also able to develop on *Symphoricarpos* (family Caprifoliaceae), the coralberry, as Voigt (1932) noted; he also observed it on the Saxifragaceae genus *Deutzia* but does not say if development was completed or not. Sich (1911) reported it on *Phyllirea media* of the Oleaceae and Kaltenbach (1874) noticed it on *Euonymus*, an ornamental temperate genus of the Celastraceae. Later, Stäger (1923) and Määr (1932) failed to rear the lilac leaf miner on this plant. I observed it on *Populus nigra*

var *italica* Muench. (Lombardy Poplar) of the Salicaceae though it did not complete development. The accidentally infested Lombardy poplars, found only twice in 1964, were in the immediate vicinity of many lilac bushes. I have observed other plants used as resting places without eggs being laid. An egg may have occasionally been carried by an ovipositing female to another plant.

TABLE 2. Average duration in days of each stage of the spring generation of *G. syringella* in 1964 and 1965.

Stage	1964		1965	
	Laboratory	Field	Laboratory	Field
Egg	6	8	5	7
1st Instar	2	3	2	5
2nd Instar	3	6	2	9
3rd Instar	7	15	7	13
4th Instar	5	5	3	5
5th Instar	4	5	2	3
Pupa	17	20	16	26
Total	44	63	37	68

TABLE 3. Average development times for the egg and larval stages of *G. syringella* during 1963, 1964, and 1965.

Year	First (Spring) Generation		Second (Autumn) Generation	
	Actual Days	Degree Days	Actual Days	Degree Days
1963	48	848	35	769
1964	42	699	49	685
1965	42	717	33	664
\bar{x} =	44	755	39	706

The Lilac and its Leaf

Lilacs are deciduous shrubs. Their leaves are opposite, petiolate, usually ovate, entire, and have reticulate venation with three to seven pairs of veins.

Gracillaria syringella is found on the leaves of the lilac, leaving the flowers untouched. The mesophyll of the lilac leaf is well differentiated into palisade and spongy parenchyma. The palisade parenchyma of two rows of closely packed, columnar cells is next to the upper epidermis. It is rich in chlorophyll and is presumably the most nutritious layer. It is mined by the most specialized first and second instar larvae. The spongy parenchyma of irregularly placed, open spaced cells is beneath the palisade layer. It does not have as much chlorophyll. This lower, more easily penetrated layer is eaten by the later instar larvae. The

mesophyll is enclosed in an epidermis that consists of a single layer of thick-walled transparent cells. On the outer surface of the epidermis, particularly on the upper surface, a waxy cuticle is secreted. The leaf is supported by a framework of veins; their hard-walled, lignin-containing cells impede the leaf miner.

Larval Adaptations for Mining

Structural differences in the larval instars correspond with variations in the habits of the larvae and with their changing environment. Generally, external feeding lepidopterous larvae have cylindrical bodies, equally wide at the fore- and hind ends. They may bear a variety of surface structures such as protuberances and bristles. Mining larvae have restricted living space and they have flattened bodies enabling them to live in the confined space of the mine. It has been shown (Hering 1951) that the flatter the mine, the flatter are the larvae. The very flat first instar larvae are found first in the lower epidermis and later in the palisade parenchyma where they apparently feed on the cell contents. The flattened second instar larvae in the palisade parenchyma also feed on cell contents. These two instars cut open a cell and suck the contents while the later tissue-feeding instars chew up entire cells. The third instar larvae have the cylindrical body form which occupies the whole space between the upper and lower epidermis. In many other mining larvae the thorax becomes heavily sclerotized but sclerotization in *G. syringella* remains weak, the fore-end of the lilac leaf miner is only slightly thickened, especially the first thoracic segment.

There are great differences between the cell-content feeding and tissue-feeding instars, primarily in the degree of flattening of the body. The changes occurring in the head region between instars two and three affect the mouthparts, the shape of the head capsule, antennae, and eyes.

Mining *G. syringella* larvae are dorso-ventrally flattened. They must feed on matter lying only in front and to the sides of them. The prognathous head position is achieved by the elongation of the labium and genae. The head is wedge-shaped and the extended mandibles at the anterior end form a point, making it much easier to penetrate the epidermal cell walls. There are no ecdysial sutures as the head capsule slips off entire, the posterior part being widest. There are only strengthening ridges present at the rear of the head (fig. 9). The antennae are situated in a protective depression behind the projecting mouthparts. There are two articles. The basal article has a very characteristic form, being slightly club-shaped and bent inwards. It has two papillae and two hairs, one very small and the other long and curved inwards at the top. The upper article is short and has two short, stout terminal bristles and one papilla (fig. 10). The ocelli are arranged in a marginal line. There are only two larger ocelli present which have moved forward slightly from the normal position for lepidopterous larvae.

In the tissue-feeding third instar the mine is more spacious and the head capsule is hypognathous (fig. 11). The larvae may eat matter beneath them as well as that lying to the sides and in front of them. The antennae have three distinct articles; the terminal one is forked at its tip, bearing on one side a conical papilla covered with sense organs and

on the other a small tactile seta, with a small hair between them. The second article has one large and two small setae and two conical sensilla. The large median seta is longer than the whole antenna and is curved in the distal one-third. There are no sensilla on the basal article (fig. 12). The grouping and number of ocelli are normal with six lying behind the mandibles in an irregular semi-circle.

Tragardh (1913) and Dimmock (1880) wrote very complete descriptions of the modifications that have taken place in the mouthparts and I will only summarize their results. The labrum of the cell-content-feeders has three to four distinct teeth on it used in cutting up the plant tissue. There is a rounded median depression (fig. 13). The mining larvae move their heads from side to side when eating, thus, from the shape of the labrum it would appear that it is used as a saw. The mandibles are horizontal and extend slightly beyond the labrum. There are two very long, narrow, pointed and closely set teeth on them. The labium is a thin lamina with an incision on the anterior margin. The hypopharynx which has merged with the labium is covered with very fine hairs. There is no spinneret and there are no labial palpi. The labium is flanked on either side by the atrophied maxillae (fig. 14).

The labrum of the tissue-feeders is plate-like, bilobed and on the edge of the ventral surface are rows of fine hairs. The labrum of the cell-content-feeders is larger than this in comparison with the size of head capsule. The mandibles of the tissue-feeders are convex. There are four teeth on the edge of the ventral surface and a fifth lies inside on the ventral surface (fig. 15). There is a spinneret present on the labium and the maxillae have the form common to lepidopterous larvae.

The modification of the larval trunk consists primarily of changes in the body extremities. The crawling locomotion in lepidopterous larvae is not possible in the confined space of the early mines. The first two instars are legless but other modifications give the larvae a degree of mobility in the mine. There are pronounced constrictions between the body segments which bulge laterally, especially in the thorax. There are numerous setae covering the body that also provide some grip on the sides of the mine. The pattern of these setae is taxonomically important as the mining larvae do not have the distinct colors and patterns of the free-living larvae. In the third instar where the depth of the mine is increased, there are both thoracic and abdominal prolegs. The thoracic ones are well developed with one pre-tarsal claw. The abdominal prolegs are on segments 3, 4, 5 and 10. They have crochets arranged in a circle with a semi-circle of crochets inside the posterior part of the circle (fig. 16). Setae are more numerous and much longer than in the cell-content feeding instars.

The Mine and Mining Operations

Mining larvae are very selective feeders, avoiding tissues such as the walls of the epidermal cells and the cuticle. They avoid the hard cells of the leaf veins and reach fresh portions of the leaf by crossing the veins near the leaf margins where they flatten out.

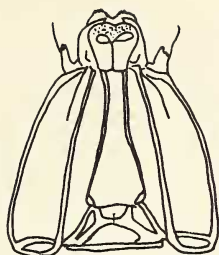


Fig. 9. Ventral view, first instar head of *G. syringella*, x 80.



Fig. 10. Antenna of first instar larva x 1300.

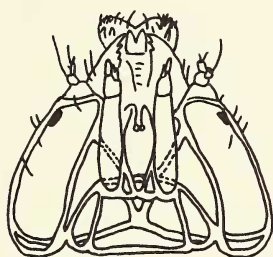


Fig. 11. Ventral view, fourth instar larva x 60.



Fig. 12. Antenna of fifth instar larva x 320.



Fig. 13. Dorsal view, labrum, first instar x 540.



Fig. 14. Dorsal view, labium, first instar x 750.



Fig. 15. Ventral view, mandible, fifth instar x 150.

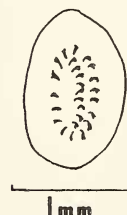


Fig. 16. Crochet arrangement on proleg, *G. syringella* larva.

The food available is largely dependent on the position of the eggs from which the larvae hatch. *G. syringella* larvae hatch from the eggs and burrow obliquely into the lower epidermis. The larvae remain as cell-contents feeders in the epidermis for part of the first instar, producing liquid excreta. The mine is very short (1 to 4 mm) and is not visible from the upper side of the leaf. From the lower epidermis the larvae again burrow obliquely through the spongy parenchyma into the palisade parenchyma and the mine becomes more apparent from the upper side than the lower. They usually stay in the second layer of palisade though they may venture into the upper row and return. They moult into the second instar and continue to mine the second row of palisade. Fragments of cell walls are consumed and pass through into the frass which becomes increasingly pellet-like though it is still only semi-solid. The frass of these first two instars is never found in the feeding area. The larva eats lying on its ventral side with its anus situated towards the center of the mine so that the mouthparts are at right angles to the mine edge. Frass is, therefore, found a length of the body away from the mine edge. This forms a distinct pattern of frass inside the mine (fig. 17). After the second moult the cylindrical third instar larvae consume both the palisade and spongy parenchyma enlarging the mine cavity rapidly. As they become tissue feeders the quantity of undigested matter in the frass increases. Hering (1951) reports frass investigations showing many substances in the parenchyma cells, e.g. some carbohydrates and mineral products, calcium oxalate and calcium carbonate are defecated without being digested. The green chlorophyll granules become darker than in living cells after passing through the digestive tract but this is only a secondary change of the chlorophyll to chlorophyllan without the larva deriving any benefit from the process. The frass is now in the form of distinct, moist pellets but the pattern present in the first two instars disappears as the pellets roll freely in the mine. The depth of the mine is increased by the consumption of the upper part of the spongy parenchyma and patches of the first and second rows of palisade. Vaulting begins with the production of silk threads which are fastened at several points to the floor of the mine. These threads contract and the roof of the mine bulges and puckers while troughs form in the floor. Frass collects in the troughs and some sticks to the silk webbing. With the moult to the fourth instar the mine becomes of full depth as all the palisade and spongy parenchyma are consumed. The result is that both mine surfaces are very thin and transparent, consisting of one epidermal cell layer. The mine is equally apparent from both surfaces. The floor and roof of the mine are both thinner so they bulge more when the silk threads strung between them contract, increasing the depth inside the mine. The depth of the mine now varies from 1 mm to 5 mm. Frass appears in larger pellets, is less moist and rolls freely around the mine. The fourth instar larvae do not stay long in the mine at this stage but eat holes through the lower epidermis and proceed out onto the surface of the leaf.

Figure 18 is an upper surface view of a small mine on a lilac leaf showing the differences in coloration in the areas mined by first to fourth instar larvae.

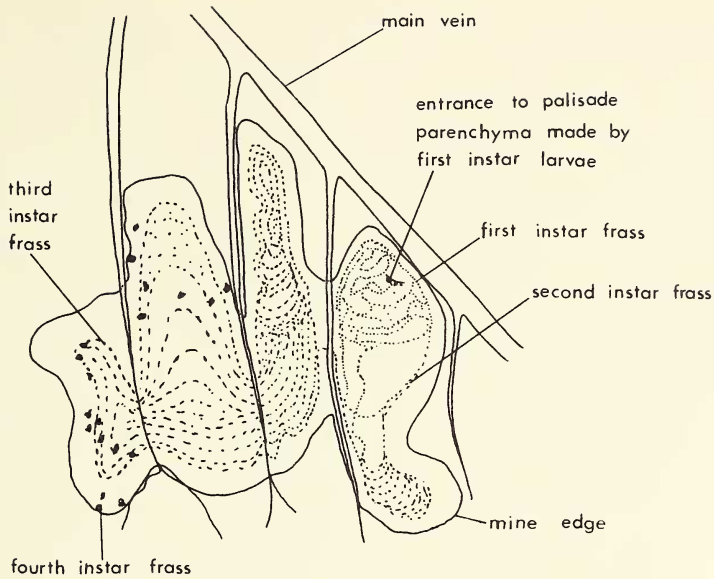


Fig. 17. Upper surface view of opened mine of *G. syringella* showing larval frass patterns $\times 7$.

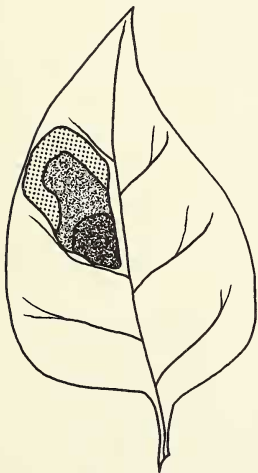


Fig. 18. Upper surface view of small mine on lilac leaf showing areas mined by first and second, third, and fourth instars respectively.

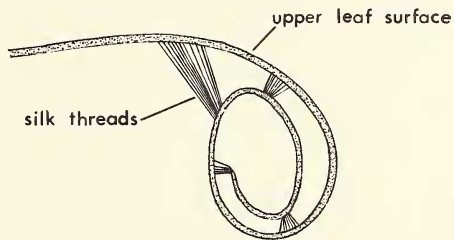


Fig. 19. Cross-section of rolled portion of a lilac leaf.

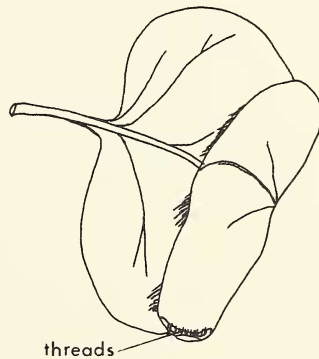


Fig. 20. Contracted silk threads closing ends of rolled leaf.

The Rolled Leaf

Fourth instar larvae chew channels across the midvein without appearing to consume the cut tissue. The cuts vary in number from one to about ten and they are between 1 mm and 10 mm apart. Rolling begins at the apex of the leaf. Silk threads are strung by the larvae from the tip on the underside of the leaf. The threads contract as they dry and the leaf tip rolls under. After these threads have fully contracted, more threads are attached from points across the middle of the roll outside to the unrolled part of the leaf. The threads are 1 mm to 7 mm long when contracted. Some larvae make only a few turns (fig. 19) while others repeat the process until the entire leaf is rolled. The ends of the roll are flattened when a series of threads strung across the openings contract, closing the apertures (fig. 18). Frass produced before the roll is completed dries out and drops out of the roll before the ends are closed. Inside the roll the larvae eat parts of all tissue except the upper epidermis. Since the larvae are usually found first in the center of the roll, all of these layers are eaten at the tip of the leaf which is rolled tightest. This is usually where the fourth instar head capsules are found after the larvae have moulted into the fifth instar. The same feeding habits are retained by fifth instar larvae which do not limit themselves to the center of the roll but eat patches throughout. The frass in the roll dries out very quickly, the pellets are loose, collecting in corners and in the webbing. When the larvae are ready to pupate they eat holes through the upper epidermis and proceed onto the outer surface of the roll. From here they descend to the ground on silk threads.

After the leaf rolling stage is reached the larvae are able to move to new, uninjured leaves which are touching their original leaves. The second leaf is tightly joined to the mined leaf with silk. Most of the rolled leaves examined had not been mined, indicating that the larvae had moved onto them in the fourth or fifth instar; 62% were rolled only, 14% were mined only and 24% were both mined and rolled.

External Appearance of Mines

The color of the mine emphasizes the details of its shape. It is usually the result of parts being eaten out of the plant tissue. Air penetrates the cavities and dries them out producing a different color from that of the rest of the leaf.

The lower epidermal mine produced by the first instar larvae, visible from the lower leaf surface only, appears a transparent yellowish color. The mine is visible from the upper surface when the first instar larvae reach the palisade parenchyma. It appears light green because of the complete or partial removal of the palisade parenchyma. It is only slightly visible from the lower leaf surface, appearing a darker green due to the presence of the spongy parenchyma.

The third instar larvae produce a mine which is increasingly conspicuous from the lower surface. The mine appears a lighter green. The full depth mine is equally apparent from both leaf surfaces as a transparent, yellowish area, since only the two epidermal layers remain.

When exit holes are produced by the fourth instar larvae, or when a hole is accidentally made in the mine, the interior dries out quickly and

turns a dark brown color. The walls shrink, become brittle and crumble easily. This also happens if the larvae die before leaving the mine, even though there are no holes present.

Changes in the Infested Leaf

Hering (1951) reports that two factors are responsible for deformities and tears in leaves of lilac, caused by mining insects: the degree of leaf development at the time of oviposition or during mine construction and the position of the mine in relation to the vascular system. I observed that the lilac leaf was very well developed before oviposition. As the leaf tissue was developed and expanded near the veins before the marginal areas and since the eggs were laid close to the veins, their presence did not stop the expansion of leaf cells. No externally visible abnormalities in leaf development could be detected. The eggs are laid along the edge of a vein, not on or inside one and the mining larvae avoid the vascular bundles so that circulation inside the veins is not interrupted. Bail (1908), in a study of plant malformations and their causes, stated that *G. syringella* larvae did cause malformations to lilac leaves. He found lobes and indentations that he thought were caused by the larvae eating the leaf, and curved leaves with damage on one margin which he said were due to young larvae eating the leaf buds but not entering them. I did not observe *G. syringella* larvae in or on leaf buds.

Deformities and tears were noticed, however, in some leaves but generally there were no mines in the deformed area. A species of the fungus genus *Phytophthora*, was found on lilac in Calgary during the summer of 1965 which caused deformities in a great many leaves. Late spring frosts may also cause localized injury by killing or splitting the tissue in the intervein areas so that later the leaves may appear as if lacerated or torn (Heald 1926). *G. syringella* seemed to avoid deformed areas of lilac leaves.

After a mine is abandoned, the thin epidermis above or below the mine is often destroyed. Air dries out the interior of the mine or dampness and rain penetrate inside the mine and produce further disintegration. Mined areas become brittle and break off in the wind. The unmined areas of the leaf remain green and alive. Abandoned mines are hiding-places for many other insects which have no direct connection with the mines and these can alter the original appearance of the mine and the leaf.

While larvae are still present in the mine or roll, particularly in the large late instars, they are hunted by birds which eat out the area of the mine or roll containing the larvae, leaving large holes and tears in the leaf.

Two or more *G. syringella* Mines in one Leaf

The female, ready to oviposit, selects a leaf large enough to serve a complete egg mass. Usually she does not deposit a second egg mass on a leaf that already has an egg mass on it. Two mines were found to occur on 13.31% of the examined mined leaves, three or more were present on 2.92% of the mined leaves. In the ovaries of field caught females there were 10-20 mature eggs present at one time, enough for

two egg masses, but egg masses found on the same leaf were usually of distinctly different ages; they were probably not laid by the same female. Different females may each successfully lay one egg mass on a single leaf. In the laboratory, females were given a choice of a clean leaf and a leaf with one egg mass already on it. These tests were inconclusive because egg masses, in addition to being deposited on the glass sides of the cages, were deposited on both the upper and lower leaf surfaces, which very rarely happens in the field.

POPULATION ESTIMATION

Percentage of Infested Leaves

The percentages of lilac leaves infested by *Gracillaria syringella* in the study area in Calgary during the spring generation of 1964 were calculated and are shown on fig. 21. The per cent infestations from 3 June to 30 June were calculated from direct counts of leaves on bushes while those from 30 June to 11 Oct. were from the collections of leaves taken for larval population samples. There was a gradual increase during the first generation as the leaves were mined and then rolled. The peak infestation was on 16 July after which there was a decrease as pupation began and new leaves were produced by the lilac bushes. The most extensively damaged of the leaves were shed, contributing to the decrease. The moths from the spring generation began to emerge and lay eggs on 27 July and the infestation from this second (autumn) generation was not noticeable until the eggs hatched and mining began. There was no noticeable increase in the percentage of infested leaves until the leaf rolling stage was reached. During the mining stage the bushes were able to produce new leaves faster than mines were formed. Plant growth slowed down in September and the bushes shed their leaves in mid-October; all the leaves were lost by 23 Oct.

Larval Populations

During the summer of 1964, 100 lilac leaves were picked every three days during the second generation as described in the section on materials and methods. The collections began on 30 June, after development was advanced and ended on 1 Oct. The average numbers of live and dead larvae per mine are shown in fig. 22. The mean number of 5.9 eggs per mass developed into larvae in the first generation. During the first generation 138 eggs were observed; 9.5% died after hatching because they came out onto the surface of a leaf. After this no other mortality factors were found and by 4 July there were still 5 live larvae per mine present. When pupation began there were 4.2 live larvae per mine, indicating a total larval mortality of 1.7 larvae per mine or 28.8%. There was a loss in numbers of live larvae in the mines from 7 July (the beginning of pupation) to 6 August because of mortality and pupation. It is difficult to separate loss by mortality from loss by pupation as the larvae drop to the ground to pupate. There was a great increase in numbers after 6 August as the eggs laid by the first generation moths hatched.

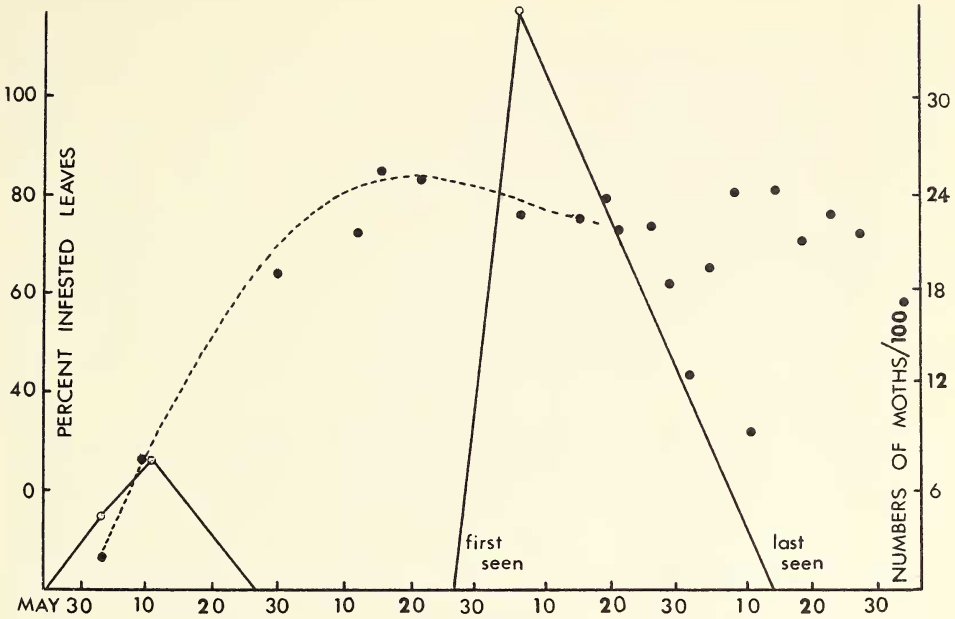


Fig. 21. Percentage of lilac leaves infested by *G. syringellae* in Calgary in 1964 (dotted line, left). Populations of moths on group A lilac bushes in Calgary in 1964 (solid line, right).

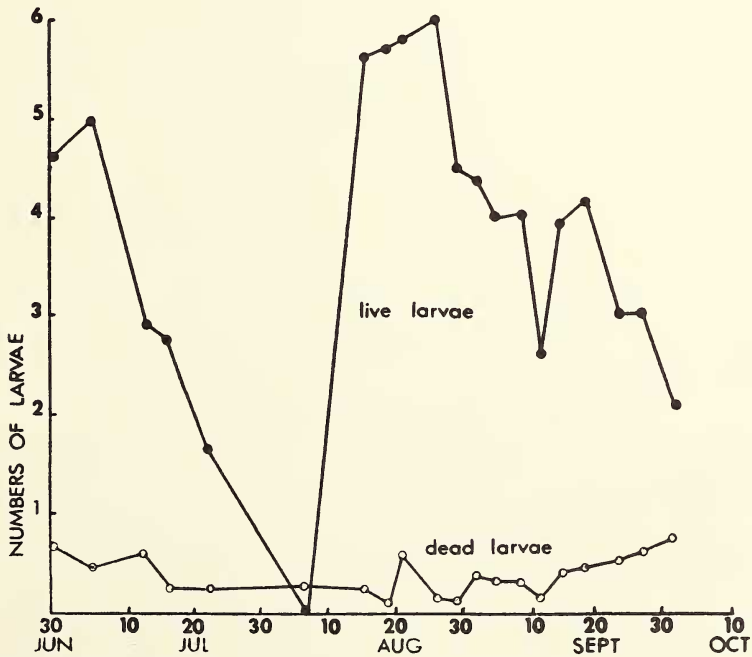


Fig. 22. Mean numbers of *G. syringella* larvae per mine collected during 1964.

The greatest average number of live larvae per mine was 6, present on 26 August. The summer generation of adults was spread out from 7 July to 15 September. The eggs took an average of 7.5 days to hatch in the field. The peak in larval numbers appears to suggest that the main batch of eggs was laid about 19 August. The loss in numbers during the following days was due to mortality. The larvae which did not succeed in entering the leaf were found near the egg masses and accounted for 7.5% of the total number of larvae. Other mortality factors are discussed below. When pupation began in the second generation there were 4 live larvae per mine, indicating a larger total larval mortality than in the spring. There was a 33% decrease from the peak number to the onset of pupation.

The numbers of dead larvae per mine were recorded. Molt skins, even the first instar head capsules, could be found in old, vacated mines. The body contents of dead larvae decayed and the remains could not be recognized more than two weeks after death, therefore, the curve is not cumulative. There are no distinct peaks in the curve showing numbers of dead larvae; at no time was there a large mortality. The slight increase in numbers of dead larvae during the last two weeks in September was due to frost kill. It is probable that frost kill was more severe than is indicated by these data because low temperatures slowed the decay and after preservation in alcohol, recently dead larvae were difficult to distinguish from those which had been living. In the field, larvae killed by frost, before decay, appeared similar to live larvae except that they were very soft. In alcohol, the softness of these larvae could not be detected.

Pupal Populations

When the first generation larvae began to pupate, 45 aluminum pie pans filled with soil were placed under the three bushes of group A, as described above. After the larvae had ceased dropping, the pans were placed individually into muslin bags and left under the bushes. The 309 moths that emerged from the pans were collected; none were from the 11 pans under the outer edges of the bushes. When emergence was over, all of the 45 pans of soil were sifted for larvae and pupae but none were found in the outer 11 pans. The other 34 pans contained 94 dead pupae; 74 bare and 20 in cocoons. No parasites were found in them. Dead larvae were not found in the soil; probably larvae which died had decayed. Moths emerged from 76.7% of the pupae. The area of the soil in the 34 pans was 11.6 sq. ft. The area of ground covered by the bushes was 75.6 sq. ft. If the sample in the pans was representative, then only 1966 moths would have emerged from the total area under the 3 bushes. The sample may not have been representative because soil-covered cocoons are almost impossible to distinguish from lumps of soil. Though the lumps in the pans were broken up, a few of the cocoons could have been missed. It was observed that some larvae wandered before burrowing into the soil. It is more likely that larvae landing in the pans would wander out, than that larvae landing on the soil surface would climb into the pans. Thus, it is probable that the pupal population estimate is low. Digging in the ground under the bushes for pupae was attempted but their

size and soil cover, plus the presence of many grass roots made it almost impossible to find them.

The pans were also placed under these bushes when the autumn generation began to pupate. The period between 14 Sept., when pupation began and 23 Oct., when all the leaves were gone off the lilac bushes, was dull, windy and wet. There were freezing temperatures on 9 days and the wind speeds were above 25 mph on 10 days. There were 1.98 inches of precipitation, including some snow. On several occasions the pans filled with water before they could be covered. The winds dried up the soil in the pans forming a hard crust that descending larvae could not penetrate. These larvae crawled over the edges of the pans and fell to the ground. During the winter the soil in these pans was sifted but little was found. Larval remains were not seen. Twenty-five of the pans had nothing in them and the other 20 had only about three pupae each, none appeared to be alive. No worthwhile estimate of pupal population could be made for this generation.

Moth Populations

The adult populations were sampled at various times during 1964 from group A bushes. An estimate of the population was made using the formula $P = NxM/R$ where, from the area selected, M is the number of moths captured, marked, and released and N is the number of moths captured on a second occasion, including R marked ones. This equation (from Andrewartha 1961) implies that the marked moths, after release, distributed themselves homogeneously with respect to the unmarked ones which were not caught and that the recapturing was done immediately after the releasing, or at least before there was time for any marked ones to die or leave the area, or for any immigrants to enter the area.

In the spring moths were marked as described in the section covering materials and methods, released in the morning and recaptured the same day. Fine days were chosen when the moths were active and the marked ones mixed in with the population quickly. The recapturing was done over the whole area of the three bushes. The adults that emerged in the spring of 1964 from overwintered pupae were samples on 3 June, 1964. The population clearly increased following this date and was re-estimated on 10 June. An estimate taken on 5 August seemed to be at the peak of the August (summer) generation of moths (Table 4). The population was obviously larger than that in the spring and a larger number of moths was marked and released.

On calm, warm days, both in bright sunshine and in the evenings the moths were easy to observe. Daily observations indicated that their numbers built up quickly and decreased gradually. A good estimate of moth longevity could not be obtained. In the field caged moths died in two days as mentioned under life cycle and habits of *G. syringella*, but conditions here were very different from those in the field. Without accurate data on longevity the total number of moths emerging in the summer of 1964 could not be calculated, but it must have been greater than the estimated peak number of 3526.

The total size of the 1964 autumn larval population was estimated. On 26 Aug., 67% of the lilac leaves in the study yard were mined and

there was an average of six larvae per mine present (fig. 22). At the end of August the number of leaves per bush in group A was estimated by counting leaves on branches of various sizes, multiplying each result by the number of branches of that size on the bushes and summing them. A total of 5870 leaves was estimated to be on the three bushes; 3933 of these were mined. As above 16.23% of the mined leaves examined had two or more mines in them, so the estimated total number of mines was 4571 and the estimated total larval population six times this or 27,426. From the section discussing fecundity in *G. syringella* the mean number of egg masses per female was 111/7 or 15. One egg mass produces one mine, so 4571 mines indicate 4571 egg masses, which could have been laid by 305 females. Thus, the total population of first generation adults necessary to produce this infestation, since the sex ratio is 1:1, would have been 610 moths. A very quick, superficial count of the moths in the area of these bushes clearly indicated a population greater than this. Large numbers of moths were very quickly counted. Neglecting the fact that some of the leaves, those shorter than 35 mm, were too small to support an egg mass, if all the leaves were mined and if every female laid 15 egg masses, a 100% infestation could be produced by only 391 females, indicating a total population of 782 moths. The eggs producing this autumn generation of larvae were laid by the 1763 females of the 1964 summer generation of 3526 moths. If this were the total population, and it is probably a low estimate as explained above, then the average number of egg masses laid per female would only have been 2.59. This is much less than the 15 egg masses they are capable of producing, therefore, the full reproductive capacity was not reached in the field.

TABLE 4. Population estimates of *G. syringella* by release and recapture.

	Moth Populations		
	Spring Emerged Moths		Summer Emerged Moths
	June 3, 1964	June 10, 1964	Aug. 5, 1964
Initially captured and marked	42	70	217
2nd capture	39	54	195
No. of marked recaptured	4	5	12
Time interval between 1st and 2nd capture	6 hr	8 hr	24 hr
Estimated population	410	756	3526

The total larval population, as calculated above, would have been 27,426 on 26 Aug., 1964. At the onset of pupation, on 14 Sept., the population had dropped to 3.98 larvae per mine, or a total population of 18,192. If all the larvae pupated successfully and survived the winter, 18,192 adults could have emerged in the spring of 1965; this is a much greater population than the 3,526 of the previous (1964) summer generation. In fact, during each of the three years of this study, the number of moths emerging in the spring was considerably smaller than the number of summer generation moths. The adult population estimate taken on 11 June, 1965 at what appeared to be the peak, indicated only 210 moths. The number of moths marked and released on 11 June was small because of the low population, therefore, the population estimate may have been inaccurate. In the spring, emergence from the overwintered pupae is more synchronous than the summer emergence; the peak estimate would include nearly the whole population. Assuming the population was 210, the overwintering mortality would have been 98.8%. This contrasts with the mortality during the pupal stage of the spring generation of 1964 which was 23.3%. As reported under pupal population estimation, the conditions at the time of pupation in the autumn of 1964 were very unfavorable, the soil surface being alternately deluged and dried to a crust. It is likely that few of the larvae managed to dig into the soil to pupate.

Mortality Factors

Parasites

Gracillaria syringella eggs did not appear to be parasitized at any time.

The rate of parasitism in *G. syringella* larvae was low. During the spring generation of 1963, 0.9% of the larvae found were parasitized, 9 parasite eggs and 9 parasite larvae were found. Larvae from the autumn generation of 1963 were not examined for parasites. During the spring generation of 1964, 0.19% of the *G. syringella* larvae examined were parasitized and during the autumn generation, of the 4,000 larvae examined, 0.15% were parasitized.

The parasite eggs included at least 5 different types, 1 internal and 4 external, which were distinguished by size, shape, and chorion pattern. Three of the 4 external parasite egg types were present only in very small numbers; 1, 2, and 4 specimens of the 3 rarer types and 42 eggs of the most common type were found. There were only 2 different types of external larvae distinguishable. One of the external larvae could be associated with its egg because 1 partly hatched larva was found and 4 mature larvae inside the chorion. The associated egg type was the one that was most numerous. An internal larva was found only in a *G. syringella* pupa.

Late in the autumn generation of 1964, on 11 Oct., ichneumonids were observed to fly around the lilac bushes. Females flew to rolled leaves and moved their antennae quickly over the surface of the roll. Then they would either oviposit into the roll, through the leaf, or move onto a new roll. Some of these rolls were examined; those they oviposited in had *G. syringella* larvae in them; those left had no larvae in them. Several of the leaves that the ichneumonids had oviposited in were

collected and kept in petri dishes in the laboratory. By 25 Nov., adults had emerged from these; they were identified by G.S. Walley as *Scambus hispae* (Harris). When the rolled leaves were opened, remains of a parasitized *G. syringella* larva and parasite pupal skins were found. The associated egg and larva mentioned above may be *S. hispae* or a close relative as the egg is similar to the description of *S. hispae* eggs given by Arthur (1963). The larvae appear similar but since they are only early instars and there has not been sufficient work done on the earlier stages of hymenopterous larvae, they could not be identified positively. No parasite pupae were found. *S. hispae* is a common external larval parasite of Lepidoptera. One *S. hispae* type larva was found in the spring generation and 16 in the autumn generation. *S. hispae* has 2 generations per year as does *G. syringella*. It is distributed from the Atlantic to the Pacific in the Canadian Transition Zone. It has never been reported on *G. syringella* before, though it has been found on other hosts in Alberta and could have moved onto the leaf miner from these. This seems to be indicated as the adult parasites were numerous yet the larval parasitism was low.

When autumn generation pupae were in the soil, on 11 October, ichneumonids were noted to be flying close to the ground and appeared to be ovipositing. Some of the ovipositing ichneumonids were collected and sent to G.S. Walley who identified them as *Itopectis quadricingulata* (Provancher). When the areas where they landed were examined, *G. syringella* pupae were found. Twenty-five of these were collected and kept in the laboratory. On 1 December they were opened; all were dried up except one in which there was a parasite larva. This was mounted and found to be in the second or third instar. The head capsule and mouthparts were different from those of the *S. hispae* type larvae. It may have been an *I. quadricingulata*, a common and widely distributed native species in North America, is an internal parasite of lepidopterous pupae. It has never been reported from *G. syringella* though it has been found in *Gracillaria* sp. on *Rosa* in Alberta.

Parasites found in Europe on *G. syringella* are listed by Fulmek (1962, appendix iv).

Predators

Ants, identified by J. Sharplin as *Formica neoclara* Emery were observed carrying *G. syringella* pupae and newly descended fifth instar larvae to their nests, at least 20 ft away from the lilac bushes. They were also seen to climb up the trunks of the lilac bushes but were not actually seen attacking larvae in the mines.

Lacewing (*Chrysopa* sp.) eggs (4) were seen on branches of lilac. They were collected and kept in a petri dish with a mined lilac leaf containing larvae. One *Chrysopa* hatched, devoured the other eggs but did not touch the *G. syringella* larvae.

A yellow warbler (*Dendroica petechia* L.) was seen by W. G. Evans to attack mined and rolled leaves, presumably to get the *G. syringella* larvae out of them. I never observed any birds attacking the lilacs but did see some marks on lilac leaves shaped like beak marks. In Europe, sparrows were reported by Pussard (1928) to be predators.

Spiders were the most numerous of the predators to be observed.

From the leaf collections preserved in alcohol of the 1963 spring generation there were indications that two species of spiders were present, identified as belonging to the Salticidae and Dictynidae. Two spider webs contained the remains of one *G. syringella* moth, one immature thrip, two acalypterate Diptera, one phorid and one nematocerate Diptera and one Hymenopteran. During the summer of 1964, preserved leaf collections contained 16 specimens representing seven families of spiders:-

- 3 Dictynidae - *Dictyna* sp.
- 1 *Dictyna annulipes* Blackwall
- 5 Theridiidae -
- 2 Salticidae - *Thiodina*
- 1 Clubionidae - *Clubiona* sp.
- 1 Thomisidae - *Philodromus aureolus* (Oliver) 1789
- 1 *Philodromus* sp.
- 1 Tetragnathidae - *Tetragnatha* sp.
- 1 Araneidae - *Acacesia* sp.

The specimen of *P. aureolus*, a male, was kept in a petri dish in the laboratory from 7 July, 1964 until death on 10 August, 1964. During this period the spider consumed $2\frac{1}{2}$ late instar *G. syringella* larvae.

Fungus

Spores and mycelia from fungi found on dead larvae and pupae were mounted in balsam; they could not be identified. From all appearances the fungi did not cause the death of the larvae but developed on them later.

Weather

Late spring frost may cause localized injury to young lilac leaves by killing or splitting the tissue in the intervein areas; later the leaves appear as if torn (Heald 1926).

Temperatures in the late autumn fluctuated very much; frosts occurred on widely scattered nights before the freezing temperatures were continuous. The first frost (Table 5) did not seem to injure the *G. syringella* larvae, though the lower temperatures slowed down their development. Continuing freezing temperatures killed larvae in the mined leaves when they were shed by the bushes on 23 October; these larvae were not far enough developed to pupate and presumably all died.

TABLE 5. Frost dates in relation to the life cycle of *G. syringella*.

Year	Emergence of First (Spring) Generation	Last Day of Frost in Spring	First Day of Frost in Autumn	Beginning of Pupation, Second (Autumn) Generation
1963	May 19	May 19	Oct. 19	Sept. 1
1964	May 26	May 26	Sept. 6	Sept. 14
1965	May 27	May 21	Sept. 5	Sept. 5

DISPERSAL

The moths marked for population studies were also used to give some estimate of dispersal. Marked moths kept in the laboratory lived as long as unmarked moths under the same conditions; an average of six days. Moths in the field were assumed to have lived at least this long or longer, and the marked ones could apparently fly as well as the unmarked ones. On 5 August 1964, 16 of a sample of 195 moths taken from the bushes of A group were marked. On 6 August, 2 out of 65 moths in the same area were found to be marked. On 8 August, three days after the initial release, one marked moth was found among 98 captures. Assuming that the marked moths were all still alive after three days and that the population remained stable with no great increases, it appears that about 90% changed bushes in the three days. Several days after all three marking experiments the surrounding bushes in the study yard, in the front yard and in the neighboring yard, were searched for marked moths. One marked moth was captured 16 ft away from the point of release and one was caught 30 ft away. Marked moths escaping into the surrounding bushes were so diluted in numbers that the chances of finding one were small.

In addition to the marking experiments, observations of the flight habits of the moths were made. Groups of between 3 and 10 moths flying around one another were often observed during the daytime to move out 5 ft or more from the bushes and return. Individual moths were seen to fly up to 50 ft away from the bushes on calm days. At the time moths were seen to fly around the bushes in great numbers; winds varied up to 15 mph. The moths stayed in the shelter of the bushes when the winds were over 20 mph. A moth outside the perimeter of a bush was quickly blown down-wind out of sight.

As reported under geographical distribution, the lilac leaf miner spread across most of the northern United States and southern Canada in recent years. This spread could have been accomplished by the moths flying, aided by wind, or some life stage being transported in lilac. Nursery stock arriving from Europe enters the country at Vancouver, Montreal and Halifax and is shipped to various points in Canada. Until recently lilacs, particularly the French hybrids, were often shipped in soil balls; pupae may have been in the soil around the roots. After May 1965, importing lilac with soil-covered roots was prohibited. They are shipped bare-rooted or in peat moss; it is unlikely that pupae are now transported in this manner. In local situations, people giving lilac bushes to their friends do not usually remove the soil from the roots; it is possible that the pupae could be carried several hundred miles or more in this way. *Gracillaria syringella*, in the leaves of bouquets of lilacs could be present in the egg and larval stages. When the flowers faded they would not be ready for pupation, therefore, the chance of spreading infestation with bouquets is small.

The moths can move a reasonably long distance without having to be transported in lilac. Along the 190 mile stretch of the #2 highway between Calgary and Edmonton, farmyards containing lilac bushes were found to be an average of 2.5 miles apart, the greatest distance between

lilac bushes was 10 miles. The moths were first recorded from Calgary in 1960; they were established by 1961 and arrived in Edmonton in 1964. The 190 miles was covered by the moths in four years, a rate of 47.5 miles per year. Meteorological data from 1964 indicated that there were only eight days a year during the moth stage on which there were south winds blowing. The average windspeed for this period was 10.4 mph; the greatest windspeed was 23 miles per hour, the winds reached 15 mph or over on six of these days. As indicated, the moths are able to fly in winds up to 15 mph but some would also fly with the wind and be aided by it. Daytime activity of the moths around the bushes is described above. At dusk they were more venturesome and flew right away from the bushes. This type of activity lasted about two hours each evening. Individuals, as mentioned previously, were able to fly at least 50 ft in one flight, without the aid of wind. A group of randomly flying moths near the northern edge of Calgary was observed; at least some were flying down-wind, aided by the wind. Under ideal conditions, if they were carried entirely by the wind, *G. syringella* moths could move, or be moved 20.8 miles, or four farms away, in one evening of flight. To move 47.5 miles would require only three evenings of wind-aided flight. Thus, the spread from Calgary to Edmonton over a four year period could be accounted for by wind-aided flight.

Gracillaria syringella was in Vancouver in 1928, in Penticton by 1941 and had reached Calgary by 1960, a period of 32 years and a distance of about 850 miles. The rate of movement was 27 miles per year. The lilac leaf miner was established in the St. Lawrence area by 1923 and had reached the coast of Maine by 1932, a distance of 320 miles moved in nine years; a rate of 35 mph. It is possible that *G. syringella* could have spread across the country by wind-borne flight alone. Whereas the lilac leaf miner was almost certainly introduced to North America in the pupal stage in soil, its rate of spread is no faster than could be accounted for by wind-aided flight.

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Note:

In 1967 the extent and severity of lilac infestations in Edmonton had greatly increased, and one specimen of ash *Fraxinus excelsior* L. adjoining a lilac *Syringa amurensis* Rupr. was found to have eggs and first or second stage mines on nearly every leaf, and on every leaflet of some leaves. Observations on September 2 however, revealed no living larvae, and no rolled leaves.

